SHORT TITLE – Hawksbill social behaviors

Interactions Among Hawaiian Hawksbills Suggest Prevalence of Social Behaviors in Marine Turtles

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ABSTRACT. – Social behaviors represent a central tenet of ecology and evolutionary biology, but remain widely undocumented in reptiles. Although marine turtles have been studied for decades, the prevalence, importance, and potential role of social behaviors have been largely overlooked. Consequently, marine turtles have predominantly been characterized as non-social animals in the literature. Here we report on visual observations of hawksbill turtles (*Eretmochelys imbricata*) inhabiting a nearshore coral reef in Hawai'i that reveal a complex array of social behaviors. Combined with recent evidence for social behaviors in other marine turtle species, our results confirm that traditional views of non-social life-histories are incomplete and that social behaviors are likely prevalent in many marine

turtle species. Our findings have important implications for marine turtle management and suggest increased research into social behaviors are warranted across the taxon.

KEY WORDS. – Animal behavior, reptiles, cheloniidae, central north Pacific, communication, cooperation.

The social behaviors of terrestrial and marine vertebrates have been studied for decades and can include tactile (e.g., caressing, hitting, biting, playing), visual (e.g. aggressive/submissive postures, courtship displays), auditory (e.g., warning cries, song communications), and chemosensory (e.g., territorial, attractant, and alarm pheromones) exchanges (Doody et al. 2012; Rubenstein and Rubenstein 2013). These behaviors support an amalgam of diverse functions, including communication, sexual selection, resource acquisition, risk avoidance, and habitat competition (Sachs et al. 2004; West et al. 2006; Noren 2008; Riesch and Deecke 2011; Breed and Moore 2012; Pitman et al. 2016; Campagna 2018). Information on social behaviors can also inform wildlife management decision making (Anthony and Blumstein 2000; Berger-Tal et al. 2015), which is particularly relevant for rare or threatened species. For instance, social animals often assemble in groups, thereby increasing their vulnerability to acute threats (Sadovy and Domeier 2005; Breed and Moore 2012).

Marine turtles represent a taxon of global conservation concern (Wallace et al. 2011; Mazaris et al. 2017). Despite the potential of social behavioral research to support marine turtle management and conservation, detailed records of social interactions in marine turtles remain extremely limited and primarily consist of behaviors associated with courtship and mating (Carr and Ogren 1960; Booth and Peters 1972; Comuzzie and Owens 1990; Miller 1997; Bevan et al. 2016; Merino-Zavala et al. 2018; Ye et al. 2020). Nonetheless, a handful of recent studies have described non-reproductive social behaviors in green turtles (*Chelonia mydas*) (Thomson et al. 2015) and, to a lesser extent, loggerhead turtles (*Caretta caretta*) (Schofield et al. 2006; Smolowitz et al. 2015). Despite these studies, literature on marine turtle life-history has largely overlooked the potential prevalence and significance of social behaviors in the taxon (Lutz and Musick 1996; Lutz et al. 2003; Wyneken et al. 2013). Correspondingly, the lack of documentation of social behaviors has led to general descriptions of marine turtles (and other

reptiles) as primarily being 'non-social' animals (Constantino and Salmon 2001; Wilkinson and Huber 2012; Doody et al. 2013).

Hawksbill turtles (*Eretmochelys imbricata*) are an endangered marine turtle species that is particularly rare in Hawai'i (Van Houtan et al. 2016; Gaos et al. 2020). Although a number of studies have described hawksbill movement, foraging, and nesting behaviors (e.g., Meylan et al. 1988; George 1997; Miller 1997; Gaos et al. 2012a), research to evaluate non-reproductive social behaviors has never been undertaken. Here we document and describe several non-reproductive social behaviors in juvenile and adult female hawksbill turtles inhabiting a nearshore coral reef in Hawai'i. To our knowledge, this is the first study to provide evidence of non-reproductive social behaviors in hawksbill turtles.

METHODS

Hawksbill Observations and Filming.—Between September 2016 and April 2020, hawksbill turtles were opportunistically observed and filmed by a local naturalist while snorkeling at a nearshore reef of approximately 30,000 m^2 in western Maui, Hawai'i. Hawksbills were captured, tagged, and measured prior to the start of the study. We determined the life-stage and sex (when possible) of turtles using a combination of carapace and tail length (Kobayashi et al. 2010), or via previous documentation of female turtles nesting on nearby beaches. When two or more turtles were observed interacting, a camera (Sony Action Cam 4K, Olympus OMD-5, or Olympus OMD-5 MKII) with underwater housing was held by the observer or placed on the ocean floor facing the turtles. The observer maintained a physical distance of >3m or quickly placed the camera on the substrate before moving away in order to minimize any disturbances or potential effects on behaviors.

Video Processing and Analysis.—Videos were visually inspected and social behavior (i.e., any physical interaction between individuals) data were logged (Table 1, Fig. 1; Supplemental Videos S1-S6), as well as the frequency of each social behavior (i.e., the number of times turtles engaged in a particular behavior). In cases where turtles mutually engaged in a behavior or where multiple behaviors were exhibited simultaneously (e.g., a turtle would Head Touch with another turtle, then one turtle would Bite), these behaviors were recorded independently. All data were tabulated, analyzed, and graphed using a combination of Microsoft

Excel (v.14.16.2) and the package ggplot2 (Wickham 2016) in the R programming language (R Core Team 2015).

RESULTS

We analyzed 10 videos involving two or more turtles, totaling 54.5 minutes of footage, of which 34.4 minutes represented time during which turtles engaged in social behaviors. We recorded a total of 149 instances of social behaviors across four turtles, which consisted of three adult females and one juvenile of unknown sex (Female 1–3 and Juvenile, respectively). All four turtles were observed repeatedly over the 3.5-year study period and Females 1–3 were previously (2015) equipped with satellite tags that transmitted for 3–11 months, during which they remained in the vicinity of the reef (PIFSC unpublished data), indicating all are resident turtles.

Head Touch (n = 66, 44.3% of observations) was the most common behavior observed, while Bite (n = 6, 4.0% of observations) was the least common (Fig. 2). The average duration of each instance of: Head Touch was 5.7 ±7.5 sec (range: 1–33 sec), Contact was 5.4 ±6.1 sec (range: 1–21 sec), Bite was 1.0 ±0.0 sec, Pursuit was 40.9 ±21.3 sec (range: 13–73 sec), Contest was 22.8 ±35.7 sec (range: 9–115 sec), and Inspect was 25.4 ±45.4 sec (range: 9–159 sec).

Two of the turtles (Juvenile and Female 1) exhibited all six behaviors, one (Female 2) exhibited five behaviors, and one (Female 3) exhibited four behaviors (Fig. 2). Interactions occurred while turtles were resting, foraging, or in transit, and were most frequently initiated by the Juvenile (n = 65), followed by Female 1 (n = 40), Female 3 (n = 32), and Female 2 (n = 12). A total of 141 interactions involved two turtles and 8 interactions involved three turtles (Supplemental Video S7). We recorded no interactions involving more than three turtles. The shortest social encounter lasted one second and consisted of a single behavior (e.g., Bite, Head Touch), while the longest encounter lasted a total of 2.7 minutes and consisted of multiple behaviors.

DISCUSSION

Although marine turtles have been studied for decades, the prevalence, importance, and potential role of social behaviors have been largely overlooked within the taxon. Our research demonstrates that Hawaiian hawksbills engage in a complex array of social behaviors, with all four turtles engaging in multiple interactions (Fig. 2). Turtles consisted of three adult females

and one juvenile residing at a foraging ground, revealing that social behaviors extend beyond courtship and mating. Our findings coincide with recent research on green and loggerhead turtles in other ocean regions (Schofield et al. 2006; Smolowitz et al. 2015; Thomson et al. 2015), suggesting that non-reproductive social behaviors may be prevalent across multiple marine turtle species and populations. The findings also indicate that traditional views of marine turtles as non-social animals are incomplete.

The limited number of studies on social behaviors in marine turtles is primarily due to the inherent difficulties of conducting such research, as most marine turtles are elusive and avoid humans (Ye et al. 2020). Marine turtles in Hawai‘i are generally habituated to human presence (Kelly and Homcy 2017), which provides valuable opportunities for first-hand observations and filming. The videos evaluated in this study were filmed by a local naturalist, without which the behavioral observations we report would have likely remained undetected. Given the limited resources available to many researchers (McNeely et al. 1990), our findings demonstrate the utility of community-based science (i.e., citizen science) approaches, which can increase the likelihood of detecting ecological patterns that could otherwise be overlooked (Tulloch et al. 2013). Although animal-borne cameras, remotely operated (underwater) vehicles (ROVs), and uncrewed aerial systems (UAS) can be used to film marine turtle behaviors (Heithaus et al. 2002; Thomson et al. 2015; Bevan et al. 2016), these techniques require some level of expertise to operate and are often prohibitively expensive.

Both green and hawksbill turtles primarily settle in neritic habitats and typically exhibit high foraging site fidelity (e.g., Seminoff et al. 2002; Makowski et al. 2006; Senko et al. 2010; Gaos et al. 2012b; Wood et al. 2017), as do some loggerhead turtle populations (Peckham et al. 2011), and thus represent relatively accessible subjects for behavioral research. Studying social behaviors of marine turtle species and populations that exhibit more vagile life-histories or that primarily forage in open-ocean habitats, such as leatherback turtles (*Dermochelys coriacea*) (Shillinger et al. 2008; Benson et al. 2011), would be considerably more challenging.

Although the overall frequency of social behaviors remains unclear, such interactions could have important management implications. If social behaviors concentrate turtles in time and space, it could increase their vulnerability to anthropogenic threats, such as directed take, fisheries bycatch, or vessel strikes (Donlan et al. 2010). Various reports of turtles observed congregating in groups of multiple individuals support this assertion (Roos et al. 2005; Bresette

et al. 2010) and could present particular threats to hawksbills, which face the added threat of being hunted for their unique shells (i.e., tortoiseshell) (Mortimer and Donnelly 2008; Miller et al. 2019; Nahill et al. 2020).

Aggressive social behaviors are often related to resource competition (Breed and Moore 2012) and the hawksbills observed in this study often engaged in Contest behavior (Table 1) near resting holes, suggesting these activities could be related to habitat competition or territoriality. Nonetheless, although some interactions appeared aggressive, others seemed innocuous. The Head Touch category (Fig. 2B, Video S1) included instances where turtles would rub the sides of their faces together or exhibit gyrating beak swipes. On multiple occasions, these interactions involved gular pumping, where turtles would use their throats to pump water in and out of their mouths and noses (Walker 1959; Owerkowics et al. 1999). Gular pumping generates a steady flow of water past the chemosensory organs and could essentially allow turtles to smell the water (Houghton et al. 2008) or in this case, each other.

Clearly, the intention, purpose, and significance of non-reproductive social behaviors in marine turtles remain unclear, but represent a relatively unexplored and fascinating line of research that would improve our understanding of marine turtle ecology. In turn, such research could support improved management decision making. Although this and previous studies (i.e., Schofield et al. 2006; Smolowitz et al. 2015; Thomson et al. 2015) on social behaviors have not evaluated the proportion of time turtles engage in social versus non-social behaviors, doing so in the future is necessary to better understand the overall pervasiveness of these behaviors.

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LITERATURE CITED

ANTHONY, L.L. AND BLUMSTEIN, D.T. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. Biological Conservation 95:303−315.

BENSON, S.R., EGUCHI, T., FOLEY, D.G., FORNEY, K.A., BAILEY, H., HITIPEUW, C., SAMBER, B.P., TAPILATU, R.F., REI, V., RAMOHIA, P., PITA, J., AND DUTTON, P.H. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. Ecosphere 2:1–27.

BERGER-TAL, O., BLUMSTEIN, D.T., CARROLL, S., FISHER, R.N., MESNICK, S.L., OWEN, M.A., SALTZ, D., ST. CLAIR, C.C., SWAISGOOD, R.R. 2016. A systematic survey of the integration of animal behavior into conservation. Conservation Biology 30:744–753.

BEVAN, E., WIBBELS, T., NAVARRO, E., ROSAS, M., NAJERA, B.M.Z., SARTI, L., ILLESCAS, F., MONTANO, J., PENA, L.J., AND BURCHFIELD, P. 2016. Using unmanned aerial vehicle (uav) technology for locating, identifying, and monitoring courtship and mating behavior in the green turtle (*Chelonia mydas*). Herpetological Review 47:27–32.

BOOTH, J. AND PETERS, J.A. 1972. Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. Animal Behaviour 20:808–812.

BREED, M.D. AND MOORE, J. 2012. Animal behavior (1st Ed). New York: Academic Press, 496 pp.

BRESETTE, M., WITHERINGTON, B., HERREN, R., BAGLEY, D., GORHAM, J., TRAXLER, S., CRADY, C., AND HARDY, R. 2010. Size-class partitioning and herding in a foraging group of green turtles *Chelonia mydas*. Endangered Species Research 9:105−116.

CAMPAGNA, C. 2018. Aggressive behavior, intraspecific. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K. (Eds). Encyclopedia of Marine Mammals (3rd Ed). New York: Academic Press, pp. 15−20.

CARR, A. AND OGREN, L. 1960. The ecology and migrations of sea turtles, 4. The green turtle in the Caribbean Sea. Bulletin of the American Museum of Natural History 121:1−48.

COMUZZIE, D.K.C., AND OWENS, D.W. 1990. A quantitative analysis of courtship behavior in captive green sea turtles (*Chelonia Mydas*). Herpetologica 46:195–202.

CONSTANTINO, M.A. AND SALMON, M. 2001. Prey detection by leatherback hatchlings. In: Coyne, M.S., and Clark, R.D. (Eds.). Proceedings of the 21st International Symposium

on the Biology and Conservation of Sea Turtles. NOAA Technical Memorandum NMFS-SEFSC-528, pp. 142–143.

R CORE TEAM. 2018. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org.

DONLAN, C.J., WINGFIELD, D.K., CROWDER, L.B., AND WILCOX, C. 2010. Using expert opinion surveys to rank threats to endangered species: a case study with sea turtles. Conservation Biology 24:1586–1595.

DOODY, J.S., BURGHARDT, G.M., AND DINETS, V. 2012. Breaking the social-non-social dichotomy: A role for reptiles in vertebrate social behavior research? Ethology 119:95−103.

GAOS, A.R., LEWISON, R.L., LILES, M., NICHOLS, W.J., BAQUERO, A., HASBÚN, C.R., VASQUEZ, M., URTEAGA, J., AND SEMINOFF, J.A. 2012a. Shifting the life-history paradigm: discovery of novel habitat use by hawksbill turtles. Biology Letters 8:54−56.

GAOS, A.R., LEWISON, R.L., LILES, M., NICHOLS, W.J., BAQUERO, A., HASBÚN, C.R., VASQUEZ, M., URTEAGA, J., AND SEMINOFF, J.A. 2012b Spatial ecology of critically endangered hawksbill turtles: Implications for conservation and management. Marine Ecology Progress Series 450:181-194.

GAOS, A.R., LACASELLA, E.L., KURPITA, L., BALAZS, G., HARGROVE, S., KING, C., BERNARD, H., JONES, T.T., AND DUTTON, P.H. 2020. Hawaiian hawksbills: A distinct and isolated nesting colony in the central North Pacific Ocean revealed by mitochondrial DNA. Conservation Genetics 21:771−783.

GEORGE, R. 1997. Health problems and diseases of sea turtles. In: Lutz, P.L., and Musick, J.A. (Eds.) The Biology of Sea Turtles, Volume 1. Boca Raton: CRC Press, pp. 363−385.

HEITHAUS, M.R., MCLASH, J.J., FRID, A., DILL, L.M., AND MARSHALL, G.J. 2002. Novel insights into green sea turtle behaviour using animal-borne video cameras. Journal of the Marine Biological Association of the United Kingdom 82:1049−1050.

HOUGHTON, J.D., CEDRAS, A., MYERS, A.E., LIEBSCH, N., METCALFE, J.D., MORTIMER, J.A., AND HAYS, G.C. 2008. Measuring the state of consciousness in a free-living diving sea turtle. Journal of Experimental Marine Biology and Ecology 356:115–120.

KELLY, I. AND HOMCY, J. 2017. Trapped in the crossroads of honu conservation. In: Mast, R.B., Hutchinson, B.J., and Villegas, P.E. (Eds.). State of the World's Sea Turtles, Volume 12. Ross: Oceanic Society, pp. 38−39.

KOBAYASHI, M., SHIMIZU, T., OKUZAWA, K., SOYANO, K., AND YOSEDA, K. 2010. Determination of maturity in male hawksbill turtle *Eretmochelys imbricata* in captivity based on tail elongation and plasma testosterone level. Fisheries Science. 76:777−784.

LUTZ, P.L., MUSICK, J.A., AND WYNEKEN, J. 2003. The Biology of Sea Turtles, Volume 2. Boca Raton: CRC Press, 472 pp.

LUTZ, P.L., AND MUSICK, J.A. 1996. The Biology of Sea Turtles, Volume 1. Boca Raton: CRC Press, 446 pp.

MAKOWSKI, C., SEMINOFF, J.A., AND SALMON, M. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas*) on shallow reef habitats in Palm Beach, Florida, USA. Marine Biology 148:1167–79.

MAZARIS, A.D., SCHOFIELD, G., GKAZINOU, C., ALMPANIDOU, V., AND HAYS, G.C. 2017 Global sea turtle conservation successes. Science Advances 3:e1600730.

MCNEELY, J.A., MILLER, K.R., REID, W.V., MITTERMEIER, R.A., AND WERNER, T.B. 1990. Conserving the world's biological diversity. Gland: IUCN, 174 pp.

MERINO-ZAVALA, A.S., RESÉNDIZ, E., HERNÁNDEZ-GIL, Y., AND LARA-UC, M.M. 2018. First report of courtship and mating behavior by loggerhead sea turtle (*Caretta caretta*) in the Gulf of Ulloa, Baja California Sur, México. Latin American Journal of Aquatic Resources 46:237−239.

MEYLAN, A. 1988. Spongivory in hawksbill turtles: a diet of glass. Science 239:393−395

MILLER, J. 1997. Reproduction in sea turtles. In: Lutz, P.L, and Musick, J.A. (Eds.). The Biology of Sea Turtles, Volume 1. Boca Raton: CRC Press, pp. 51−81.

MILLER, E.A., MCCLENACHAN, L., UNI, Y., PHOCAS, G., HAGEMANN, M.E., AND VAN HOUTAN, K.S. 2019. The historical development of complex global trafficking networks for marine wildlife. Science Advances 5:eaav5948.

MORTIMER, J.A. AND DONNELLY, M. 2008. Marine Turtle Specialist Group 2007 IUCN Red List Status Assessment Hawksbill Turtle (*Eretmochelys imbricata*). http://www.iucn-mtsg.org/red_list/ei/index.shtml.

NAHILL, B., VON WELLER, P., AND BARRIOS-GARRIDO, H. 2020. The global tortoise shell trade. Seeturtles.org Report, 83 pp.

NOREN, S.R. 2008. Infant carrying behaviour in dolphins: Costly parental care in an aquatic environment. Functional Ecology 22:284−288.

OWERKOWICZ, T., FARMER, C.G., HICKS, J.W., AND BRAINERD, E.L. 1999. Contribution of gular pumping to lung ventilation in monitor lizards. Science 284:1661–1663.

PECKHAM, S.H., MALDONADO-DIAZ, D., TREMBLAY, Y., OCHOA, R., POLOVINA, J., BALAZS, G., DUTTON, P.H., AND NICHOLS, W.J. 2011. Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. Marine Ecology Progress Series 425:269–280.

PITMAN, R.L., DEECKE, V.B., GABRIELE, C.M., SRINIVASAN, M., BLACK, N., DENKINGER, J., DURBAN, J.W., MATHEWS, E.A., MATKIN, D.R., NEILSON, J.L., SCHULMAN-JANIGER, A., SHEARWATER, D., STAP, P., AND TERNULLO, R. 2016. Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism? Marine Mammal Science 33:7–58.

RIESCH, R. AND DEECKE, V.B. 2011. Whistle communication in mammal-eating killer whales (*Orcinus orca*): Further evidence for acoustic divergence between ecotypes. Behavioral Ecology and Sociobiology 65:1377–1387.

ROOS, D., PELLETIER, D., CICCIONE, S., TAQUET, M., AND HUGHES, G. 2005. Aerial and snorkeling census techniques for estimating green turtle abundance on foraging areas: a pilot study in Mayotte Island (Indian Ocean). Aquatic Living Resources 18:193–198.

RUBENSTEIN, D.I. AND RUBENSTEIN, D.R. 2013. Social behavior. In: Levin, S.A. (Eds). Encyclopedia of Biodiversity (2nd Ed). Waltham: Elsevier/Academic, pp. 571-579.

SACHS, J.L., MUELLER, U.G., WILCOX, T.P., AND BULL, J.J. 2004. The evolution of cooperation. The Quarterly Review of Biology 79:135−160.

SADOVY, Y. AND DOMEIER, M. 2005. Are aggregation fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254−262.

SCHOFIELD, G., KATSELIDIS, K.A., DIMOPOULOS, P., PANTIS, J.D., AND HAYS, G.C. 2006. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. Endangered Species Research 2:71−79.

SEMINOFF, J.A., RESENDIZ, A., AND NICHOLS, W.J. 2002. Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Marine Ecology Progress Series 242:253–65.

SENKO, J., KOCH, V., MEGILL, W.M., CARTHY, R.R., TEMPLETON, R.P., NICHOLS, W.J. 2010. Fine scale daily movements and habitat use of East Pacific green turtles at a shallow coastal lagoon in Baja California Sur, Mexico. Journal of Experimental Marine Biology and Ecology 391:92–100.

SHILLINGER, G.L., PALACIOS, D.M., BAILEY, H., BOGRAD, S.J., SWITHENBANK, A.M., GASPAR, P., WALLACE, B.P., SPOTILA, J.R., PALADINO, F.V., PIEDRA, R., ECKERT, S.A., AND BLOCK, B.A. 2008. Persistent leatherback turtle migrations present opportunities for conservation, PLOS Biology. 6:e171.

SMOLOWITZ, R.J., PATEL, S.H., HAAS, H.L., AND MILLER, S.A. 2015. Using a remotely operated vehicle (ROV) to observe loggerhead sea turtle (*Caretta caretta*) behavior on foraging grounds off the Mid-Atlantic United States. Journal of Experimental Marine Biology and Ecology 471:84−91.

THOMSON, J., GULICK, A., AND HEITHAUS, M. 2015. Intraspecific behavioral dynamics in a green turtle *Chelonia mydas* foraging aggregation. Marine Ecology Progress Series 532:243−256.

TULLOCH, A.I., POSSINGHAM, H..P, JOSEPH, L.N., SZABO, J.K., AND MARTIN, T.G. 2013. Realising the full potential of citizen science monitoring programs. Biological Conservation 165:128–38.

VAN HOUTAN, K.S., FRANCKE, D.L., ALESSI, S., JONES, T.T., MARTIN, S.L., KURPITA, L., KING, C.S., AND BAIRD, R.W. 2016. The developmental biogeography of hawksbill sea turtles in the North Pacific. Ecology and Evolution. 6:2378–2389.

WALLACE, B.P., DIMATTEO, A.D., BOLTEN, A.B., CHALOUPKA, M.Y., HUTCHINSON, B.J., ABREU-GROBOIS, F.A., MORTIMER, J.A., SEMINOFF, J.A., AMOROCHO, D., BJORNDAL, K.A., BOURJEA, J., BOWEN, B.W., DUEÑAS, R.B., CASALE, P., CHOUDHURY, B.C., COSTA, A., DUTTON, P.H., FALLABRINO, A., FINKBEINER, E.M., GIRARD, A., GIRONDOT, M., HAMANN, M., HURLEY, B.J., LÓPEZ-MENDILAHARSU, M., MARCOVALDI, M.A., MUSICK, J.A., NEL, R., PILCHER, N.J. TROËNG, WITHERINGTON, B., AND MAST, R.B. 2011. Global conservation priorities for marine turtles. PLOS ONE. 6:e24510.

WALKER, W.F. 1959 Closure of nostrils in the Atlantic loggerhead and other sea turtles. Copeia 1959:257–259.

WEST, S.A., GRIFFIN, A.S., AND GARDNER, A. 2006. Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. Journal of Evolutionary Biology 20:415−432.

WICKHAM, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

WILKINSON, A. AND HUBER, L. 2012. Cold-blooded cognition: reptilian cognitive abilities. In: Vonk, J., Shackelford, T.K. (Eds.). The Oxford Handbook of Comparative Evolutionary Psychology. Oxford: Oxford University Press, pp. 129−143.

WOOD, L.D., BRUNNICK, B., AND MILTON, S.L. 2017. Home range and movement patterns of subadult hawksbill sea turtles in Southeast Florida. Journal of Herpetology 51:58-67.

WYNEKEN, J., LOHMANN, K.J., AND MUSICK, J. 2013. The Biology of Sea Turtles, Volume 3. Boca Raton: CRC Press, 475 pp.

YE, M., CHEN, H., LI, M., DUAN, J., AND LI, P. 2020 Observations on the courtship and mating behavior of captive green turtles (*Chelonia mydas*). Herpetological Conservation and Biology 15:284−292.

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Table 1. Social behavior categories used to classify hawskbill turtle interactions in Maui, Hawai‘i. With the exception of some phases of the Pursuit category, all social interactions consisted of turtles in close proximity (<1m).

Behavior	Description
Head Touch*	Touching, rubbing or striking heads together; includes gyrating beak swipes and gular pumping
Contact	Any physical contact between two or more turtles aside from Head Touch or Bite
Bite*	A turtle biting any part of another turtle
Pursuit	Purposeful pursuit by one turtle of another turtle
Contest^	Aggressive interaction, could involve Head Touch, Bite, or Pursuit
Inspect*	Non-aggressive interaction without physical contact

*Adapted from Thomson et al. 2015; ^Adapted from Schofield et al. 2006

Figures

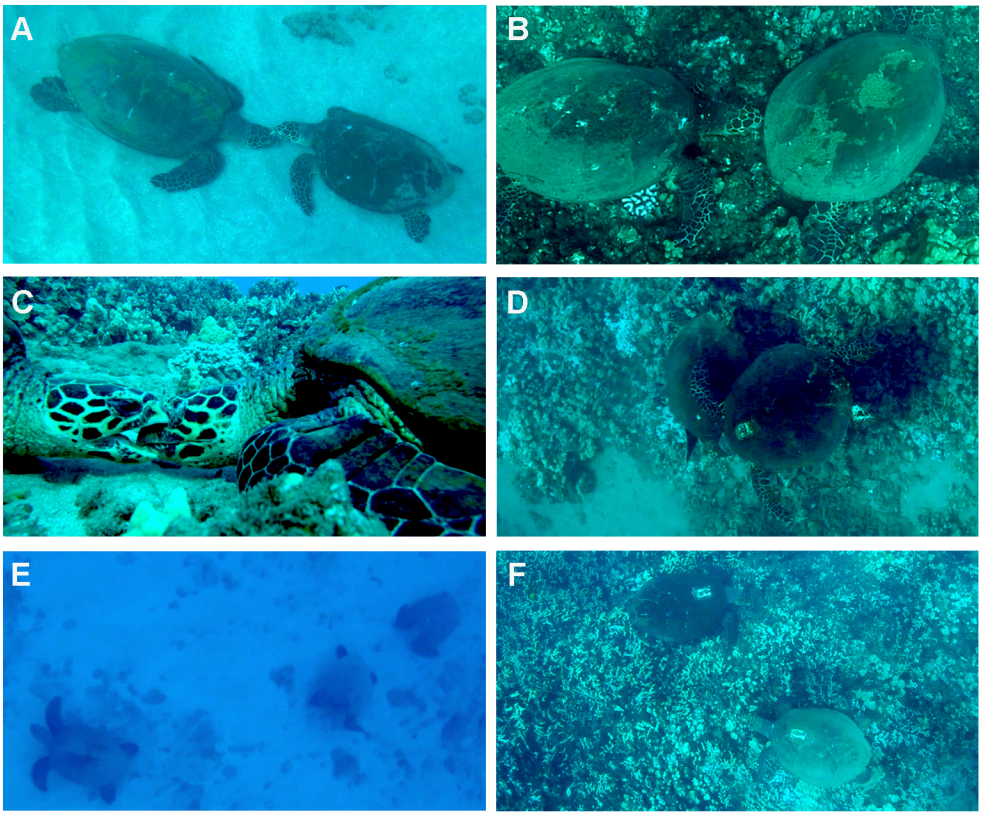

Figure 1. Images of behaviors exhibited by hawksbills, including (A) Head Touch (Video S1), (B) Contact (Video S2), (C) Bite (Video S3), (D) Contest (Video S4), (E) Pursuit (Video S5), (F) Inspect (Video S6). Photo credit: Don McLeish.

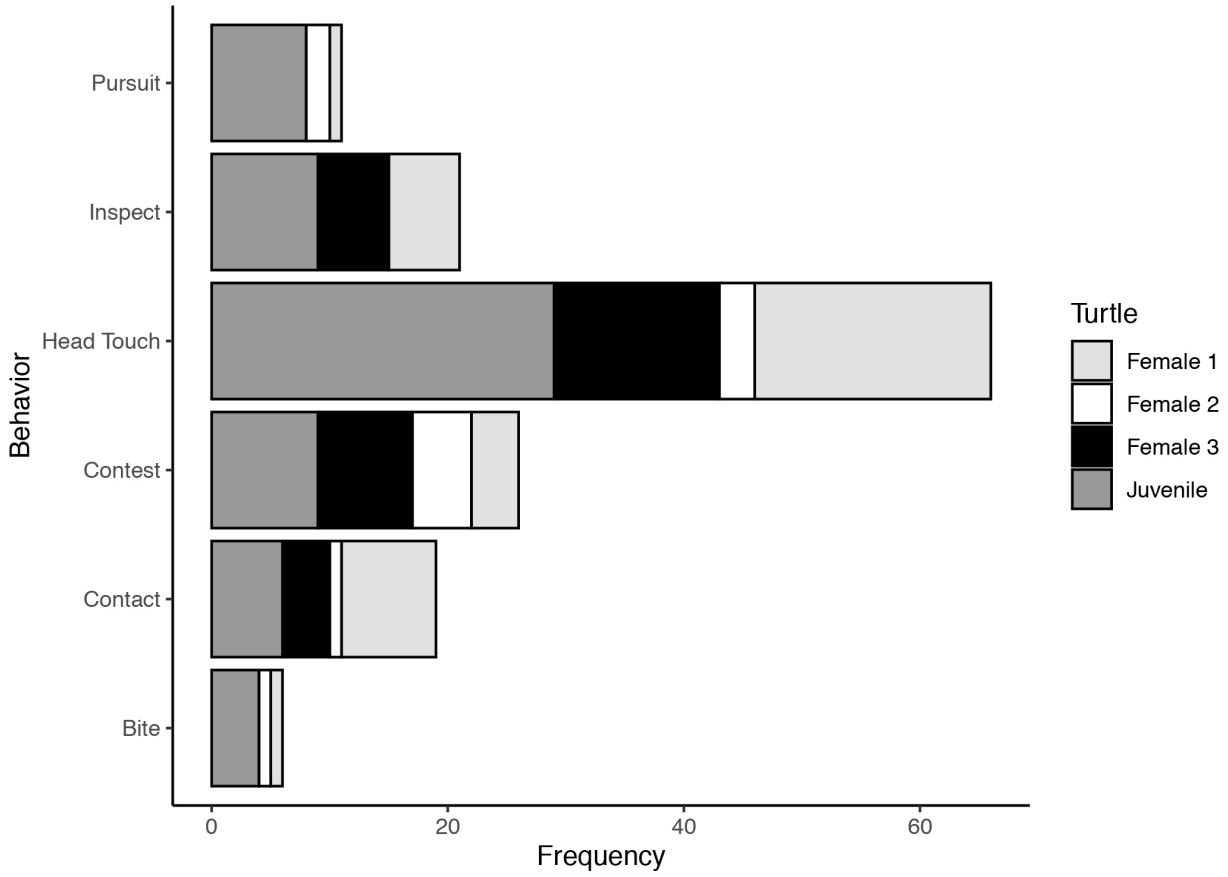

Figure 2. The frequency each of the four hawksbill turtles exhibited the social behaviors recorded during this study.

Supplemental videos: Below are links, titles, and captions for the seven supplemental videos referenced in the manuscript. Video credits: Don McLeish.

Video S1 - https://youtu.be/87lMNi7eS3c

Title: Head Touch behavior

Legend/Caption: Video of the Head Touch behavior, which includes touching, rubbing or striking heads together, as well as gyrating beak swipes and gular pumping

Video S2 - https://youtu.be/qNFSK63LVyM

Title: Contact behavior

Legend/Caption: Contact behavior, which includes any physical contact between two or more turtles that did not involve Head Touch or Bite

Video S3 - https://youtu.be/QrKj9IEEpGs

Title: Bite behavior

Legend/Caption: Bite behavior, which includes a turtle biting any part of another turtle

Video S4 - https://youtu.be/KVORQoYqYiM

Title: Pursuit behavior

Legend/Caption: Pursuit behavior, which includes the purposeful following by one turtle of another turtle

Video S5 - https://youtu.be/v52IQ2vKLh0

Title: Contest behavior

Legend/Caption: Contest behavior, which includes an aggressive interaction, not including Head Touch, Bite or Pursuit

Video S6 - https://youtu.be/b8HO7_-oz_s

Title: Inspect behavior

Legend/Caption: Inspect behavior, which includes a non-aggressive interaction without physical contact

Video S7 - https://youtu.be/duriYo0Z0sU

Title: Three turtles interacting

Legend/Caption: Three hawksbill engaging in social behaviors